Chapter 6
Timing Matters: Allochronic Contributions to Population Divergence

Barbara Helm and Robyn Womack

Abstract Globally, most birds reproduce to some extent seasonally, and the timing of their annual breeding events involves regulation by biological clocks. Biological clocks also regulate diel activities, including song and other courtship behaviors which occur at certain times of day. Differences between individuals in the timing of display and breeding (i.e., allochrony) can drive genetic divergence, contribute to isolation between populations, and ultimately lead to speciation. Isolation by breeding time is thought to be common in areas where reproductive seasons differ greatly over short distances, for example in tropical regions. Here we introduce the ways biological clocks of birds function, and review evidence for variation between individuals and between populations. The potential importance of allochrony for the speciation of birds is underpinned by the periodic growth and regression of their reproductive organs, by their rigid migration programs, and possibly also by their learnt, well-timed mating behaviors (in particular song). We exemplify isolation by time in tropical songbirds and in migratory species. Potentially, further contexts that could promote allochronic isolation in birds include the differentiation between urban and rural populations, as urbanization is commonly associated with modified timing of breeding and song.

Keywords Isolation by time · Biological rhythm · Circannual · Circadian · Seasonality · Chronotype · Assortative mating · Song · Tropical · Migration

6.1 Timing Is Everything!

A number of environmental rhythms repeat faithfully and are highly predictable, because they arise from astronomical cycles. These include annual and daily rhythms caused by the orbit of the Earth around the Sun and the rotation of the

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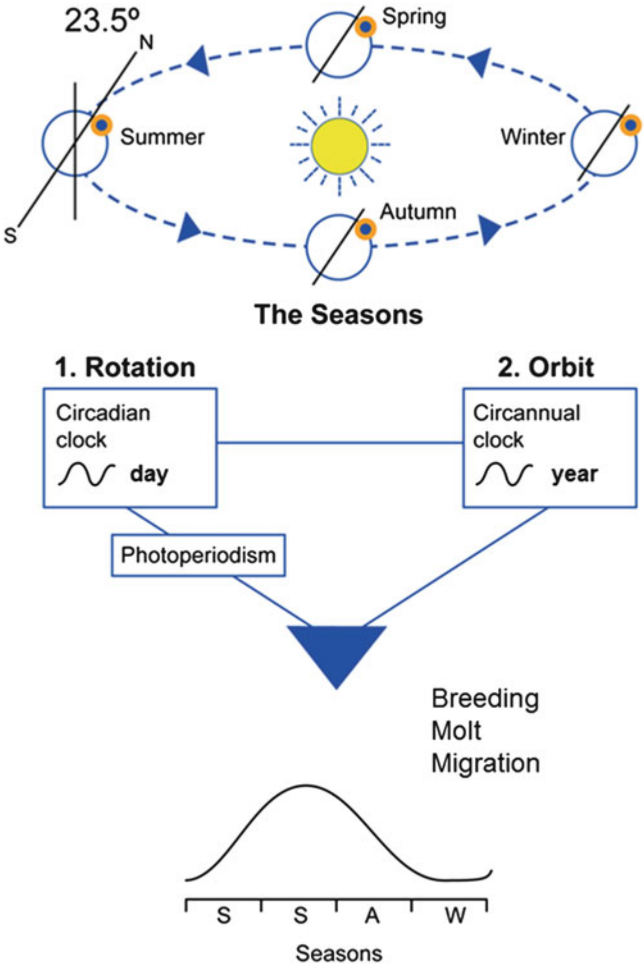

Fig. 6.1 Diel timing every 24 hours aligns with the rotation of the Earth (line S/N indicates the rotational axis, and the filled circle represents a specific time point of reference) and annual timing aligns with the Earth's orbit around the Sun every 12 months (shown by the eclipse). These astronomical cycles have favored the evolution of internal circadian (approximately daily) and circannual (approximately annual) clocks. Circadian rhythms regulate the timing of many daily activities, including song and courtship. For annual timing, the ability to respond to changes in day length (photoperiodism) depends on the circadian clock system. Birds utilize both types of internal, innate timing mechanism to regulate reproduction, molt, migration, and other processes [adapted from Helm and Lincoln (2017)]

Earth around its axis (Fig. 6.1). Likewise, the orbit of the Moon around the Earth shapes lunar and tidal rhythms. Many humans underestimate the challenges of living in a deeply rhythmic world, because they can extend their day into the night using artificial lights and are sheltered from cold, rain, and storms by housing, heating, and protective gear. In contrast, for a bird, a temperate-zone forest is a very different habitat at night than at daytime and during the summer compared to winter (Foster and Kreitzman 2005; Helm and Lincoln 2017). Changes in its environment include those in abiotic factors like light and temperature, in biotic opportunities and risks like food availability and exposure to predators and parasites, and in social factors like its forest bird community and the behavior of its conspecifics (Helm et al. 2006, 2017). Likewise, for a bird in a tropical forest or savannah, alternation between dry and rainy seasons can also fundamentally modify its habitat (Moore et al. 2005; Goymann and Helm 2014). It is therefore unsurprising that birds have structured their lives by these rhythms. Because the many, sometimes competing, demands on timing require careful balancing, species, populations, and individuals within populations may differ in the precise solution of timing challenges.

In this chapter, we argue that biological timekeeping, in particular on an annual and daily time scale, can promote isolation between differently timed individuals and can be a driver of the diversification of birds (Hendry and Day 2005; Taylor and Friesen 2017). We will first introduce basic background on biological rhythms and then demonstrate the diversity of avian timing, highlighting putative isolation mechanisms.

6.2 Clockworks

Because astronomically based environmental rhythms are so predictable (Fig. 6.1), organisms have evolved a range of preparatory strategies for coping with them. A big step early in the evolution of life (Hut and Beersma 2011) was anticipation of environmental changes, when cyanobacteria progressed from simply reacting to periodical changes to predicting them in advance. Since then, organisms have evolved sophisticated behaviors that rely on precise prediction of the periodic changes in the environment. For example, many migratory bird species leave their breeding grounds before they become inhospitable, and initiate their return movements in anticipation of the upcoming spring (Numata and Helm 2014). Likewise, birds are usually not simply woken by morning twilight but will have anticipated the upcoming day well in advance (Foster and Kreitzman 2005).

The remarkable achievement of anticipation is possible, because birds, like other organisms, have internalized timekeeping. They have evolved body clocks (referred to as biological rhythms) that are innate and thereby part of their inheritance from generation to generation. These clocks tick on even if the birds are sheltered from environmental changes, for example in a continuously lit room or under the continuous light of polar summer days (Foster and Kreitzman 2005; Ashley et al. 2014; Helm and Lincoln 2017). Birds will alternate each day between activity and rest, their body temperature will rise and fall, and they may rhythmically show behaviors, for example crowing, even under constant conditions (Shimmura and Yoshimura 2013; Shimmura et al. 2015). However, these biological clocks run at their own, internal speed, which often makes them drift a bit. If a bird cannot experience environmental cycles, its biological rhythm is usually somewhat faster, or slower, than the corresponding environmental cycles (hence, it is called a “circa” rhythm).

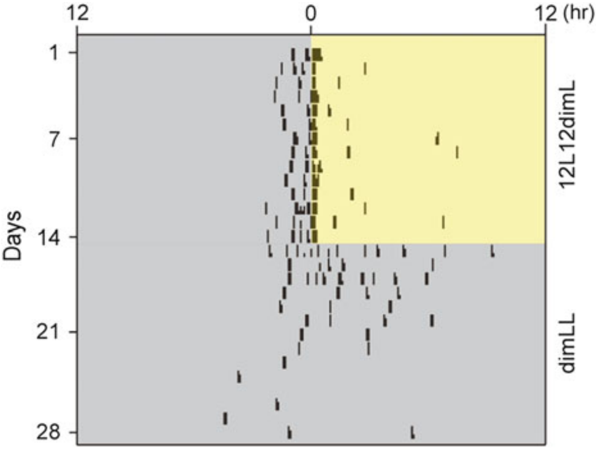

Fig. 6.2 Circadian regulation of rooster crowing. The figure shows crowing of a rooster (black marks) over 4 weeks. First, the bird was recorded under cycles of 12 hours of light followed by 12 hours of dimmed light at night, indicated by yellow and gray backgrounds, respectively. Then, the bird was recorded under constant conditions of dim light (gray background only). The onset of its crowing became progressively earlier under constant conditions. Time "0" on the *x*-axis shows start of light; time points "12" mark 12 hours before and after the start of light. Each line in the graph (*y*-axis) shows a day of recording [adapted from Shimmura and Yoshimura (2013), Shimmura et al. (2015)]

The best-known biological rhythm is that of the circadian clock which drives timing across the 24-hour day. This can be seen in Fig. 6.2 which shows the time of crowing in a rooster. While the rooster experiences changes between light (indicated by the yellow box) and darkness, it always starts crowing at a similar time of day, somewhat before dawn. But once the light is kept constant, the rooster crows a bit earlier each morning, and its rhythm drifts. This drift can be measured as the "period length" of a rooster, i.e., the time taken from one cycle (start of crowing) to the next. In Fig. 6.2, the rooster's clock is faster than 24 hours, and hence, it has a shorter period length. In their natural environment, such fast-clocked individuals are usually particularly early risers, whereas slow-clocked individuals tend to be late risers (Dominoni et al. 2013b).

For the circadian clock, the mechanisms that drive this rhythm have been intensively studied, highlighted by the recent award of the 2017 Nobel Prize in Physiology or Medicine. We now know that rhythms are generated within cells by a loop of so-called clock genes, which switch each other on and off to measure out the period of circa 24 hours. Many other genes are involved, for example by linking clocks to metabolism. Then, the millions of cellular clocks in a bird, fly or human need to be coordinated to produce useful body time. This is achieved, for example by nerve-cell coupling in brain centers and by hormones, such as melatonin which peaks at night (Foster and Kreitzman 2005). Through various links and feedback loops, organisms thus achieve coordinated rhythms within their bodies. Because clocks are so important to the life of organisms, they are very sensitive to important cues from the environment, in particular to changes of light and darkness. Birds perceive these changes and adjust ("synchronize") their biological rhythms so that they match the 24-hour daily cycle of the environment (Fig. 6.2).

Although only circadian rhythms are understood in detail, the same principles hold for cycles on other time scales (Numata and Helm 2014). Recent, exciting breakthroughs have shed light on circatidal clocks, which help coastal organisms anticipate the rising and falling of marine water levels (Zhang et al. 2013; Kaiser et al. 2016), and circalunar clocks, by which organisms anticipate the waxing and waning of the Moon (Zantke et al. 2013). Finally, the rhythms that relate most directly to avian reproduction are circannual rhythms (cycles repeating with a period length of circa one year; Gwinner 1986, 1996; Helm and Lincoln 2017). Circannual rhythms can regulate many processes, including preparations for breeding, molt, and migration. Most avian species breed at least to some extent seasonally (Goymann and Helm 2014). Likewise, birds generally molt at least once per year to replace their feathers, and many species carry out regular migrations which are often precisely timed (Gwinner 1996; Battley 2006; Helm et al. 2006; Newton 2008). Associated with their aerial lifestyle, birds undergo extreme annual changes: for example, they greatly reduce their reproductive organs (testes of males, ovaries and oviducts of females; Williams 2012) outside the breeding seasons. In small songbirds, testes typically grow to diameters of 0.5 cm during breeding but shrink in winter to below 10% of this size and contain no sperm (Helm 2009; Williams 2012). This makes reproduction in birds generally highly seasonal, preventing many species from spontaneously breeding, for example during warm weather in winter or after migrating to tropical areas. An example for innate circannual rhythms in reproductive condition is shown in Fig. 6.3 for Eurasian Blackcaps *Sylvia atricapilla*.

As described above for circadian rhythms, circannual cycles also typically continue if a bird is prevented from witnessing environmental changes (Gwinner 1996; Goymann and Helm 2014). For example, in stonechats (songbirds within the genus *Saxicola*), the growth and reduction of reproductive organs is driven by a circannual clock. When pairs were kept in aviaries under constant day length of 12 hours of light alternating with 12 hours of night, males and females reproduced if they came into reproductive condition at similar times (Gwinner 1996; Goymann and Helm 2014). Their sons and daughters never experienced rhythms in their environment, but nonetheless showed annual cycles of breeding condition and molt, driven by their circannual clocks. Under these conditions, breeding condition of the stonechats drifted from the annual cycle of 365 days, much like the crowing behavior of the rooster drifted from the 24-hour cycle shown in Fig. 6.2. Under natural conditions, circannual rhythms like circadian rhythms synchronize to environmental cycles (Gwinner 1986; Helm and Lincoln 2017). The most important synchronizing cue on an annual time scale is photoperiod (day length), although other cues can also play a role (Helm et al. 2006; Goymann and Helm 2014).

The precise timing of behavior and activities of birds under natural conditions is influenced by many additional factors that modify the outcome of biological timekeeping. For example, the time of song and breeding can be influenced by age,

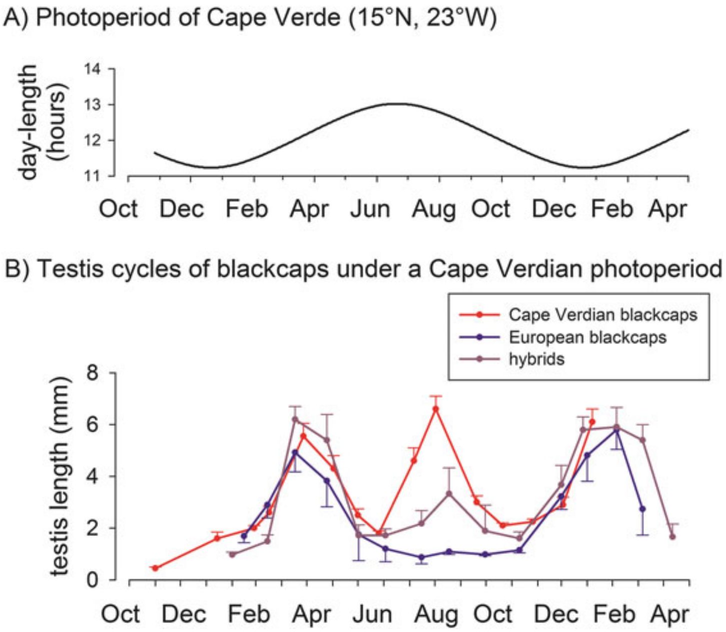

Fig. 6.3 Innate, internal cycles of testis growth and regression in male Eurasian Blackcaps *Sylvia atricapilla*. Blackcaps on the Cape Verde islands go through two reproductive cycles per year, whereas European Blackcaps go through one annual cycle. In captivity, the birds show the time patterns of their native populations, and hybrids are intermediate. Male Blackcaps were kept under the photoperiodic condition of the Cape Verde islands. (**a**) Number of daylight hours. (**b**) Testicular cycles of Blackcaps from Cape Verde (red), southern Germany (blue), and hybrids (purple) of the two populations maintained under identical conditions [data from Berthold and Querner (1993), figure adapted from Goymann and Helm (2014)]

experience, dominance, body condition, and various local environmental factors (Poesel et al. 2006; Helm et al. 2006; Shimmura et al. 2015). But importantly for the subject of avian speciation, innate biological rhythms provide a powerful substrate for evolutionary change (Fig. 6.3; Helm and Visser 2010; Taylor and Friesen 2017).

6.3 Allochrony: Differences in Timing Between Individuals, Populations, and Species

Birds that differ from each other in reproductive timing are said to be "allochronic" (i.e., they diverge in timing; Taylor and Friesen 2017). In the above description of clockworks, we explained that individuals may display consistently early or late timing behavior, captured by the term "chronotype" (Hau et al. 2017; Helm et al. 2017). Such variation is found between individuals, between populations, and

Fig. 6.4 Chronotype of individual songbirds schematically depicted against the backdrop of a Scottish forest woodland. The image shows three individuals during early morning hours which differ slightly from each other in their biological clock times (depicted by a clock imposed on each bird's head). For two of these individuals, subjectively, the time for starting dawn song (set to just after 03:00 hours in May in Scotland) is yet to come. The third individual, in contrast, has a slightly earlier biological rhythm. For this bird, the time for initiating song has already started (depicted by its biological clock showing 03:05 hours), and the bird is accordingly singing. Original artwork: Robyn Womack

between species. Within populations, some individuals are typically the first to become active in the morning, while others may start later but extend their activities into the evening. This is illustrated in Fig. 6.4, which schematically shows three conspecifics at the same time in the same forest patch. The three birds differ slightly in their biological rhythm, with their chronotype highlighted as clock time. Similarly, on an annual time scale, some individuals come into reproductive condition or return from migration early in the year, whereas others might be timed later. On both diel and annual time scales, there is evidence that individual differences are heritable (e.g., Nussey et al. 2005; Helm and Visser 2010; Caprioli et al. 2012).

Timing differences between individuals can have important reproductive consequences. Courtship and reproductive behaviors are often fitted to short phases of conducive environmental conditions. Therefore, reproductive success can differ between individuals performing these behaviors early or late in the day or year (Hau et al. 2017). For example, in Fig. 6.4, the bird whose clock is the most advanced is already singing, while the others are still preparing for the day. Several studies have shown that a male that starts dawn song particularly early in the day has high chances of enjoying increased reproductive success (Poesel et al. 2006; Hau et al. 2017). A recent review article (Hau et al. 2017) discusses to which extent the timing of behaviors may therefore be under sexual selection. As detailed by Hau and colleagues, for the timing of behaviors such as song to be a candidate for sexual selection, it would need to increase matings but also impose a cost on the singing bird (e.g., shortened sleep duration). For sexual selection to take effect, there also needs to be a genetic contribution to the specific timing of an individual, which can then be modified by evolution (Helm and Visser 2010). Clock genes, and potentially their epigenetic modification, have been shown to play a role in such modifications in a number of taxa (Caprioli et al. 2012; Hau et al. 2017; Taylor and Friesen 2017; Saino et al. 2017).

However, sexual selection is not the only factor that could drive and maintain genetic variation in the timing of individuals. It is very likely that there are also other pressures, such as natural selection for greater fecundity or survival (Hau et al. 2017). For example, for both males and females, waking early could enable improved feeding opportunities, and an early return from migration could provide access to superior breeding territories (Bearhop et al. 2005; Hau et al. 2017). Thereby, individuals which due to a mutation rise or return earlier could enjoy greater fecundity or survival. Maintaining diversity in timing however requires that such benefits are not universal. For example, early risers may sometimes suffer energetic costs on brisk mornings or predation by nocturnal predators, counterbalancing natural selection for earlier onset of activity. Likewise, early-returning migrants can get caught in severe weather in late winter, from which late-returning migrants are spared (Newton 2008). A role of biological clocks in the contexts of sexual and natural selection has been demonstrated in a range of organisms, especially in insects and fish (Kaiser et al. 2016; Taylor and Friesen 2017).

For variation between individuals to drive divergence within a population, there must be isolating mechanisms. For example, because reproductive behaviors often occur during short phases only, males and females that are similarly timed might preferentially mate with each other (Fig. 6.4). Such "assortative mating" could then accelerate genetic changes in the clockworks, further driving divergence within a population (Bearhop et al. 2005; Dominoni et al. 2013a, b). An example is once again Blackcaps (Bearhop et al. 2005). In this species, some individuals began making a genetically determined shorter migration journey and returned to the breeding grounds earlier in the spring (Newton 2008). Males and females carrying out this shorter migration preferentially mated with each other soon after arrival on the breeding grounds, before conspecifics taking a longer route arrived (Bearhop et al. 2005). This difference in mating times could have contributed to the observed, fast spread of the novel migration behavior.

Variation in chronotype within populations connects seamlessly to differences between populations, if time-structuring factors isolate parts of a population from others. Migration, as described above, can be one such factor. Others can be important ecological factors that differ in timing. Here, the most convincing examples come from insects, for example, from fruit flies that have specialized on host plants that differ in timing of fruition (Taylor and Friesen 2017). In birds, most examples of allochronic divergence involve some separation in space at the time of breeding. Spatial distances do not need to be large because habitats can differ in optimal timing even over short distances, for example in tropical environments.

Thus, breeding timing differs dramatically between populations of Rufous-collared Sparrows *Zonotrichia capensis* that breed on the western and eastern slopes of the Ecuadorian Andes, which in turn differ in the timing of rainy seasons (Moore et al. 2005). These populations do not overlap in the timing of breeding and have already started to diverge (see below).

On larger spatial scales, populations may differ systematically in reproductive timing, for example across latitudinal gradients, where more northerly breeding populations typically reproduce later in the year (Helm 2009). One extreme example is stonechat populations from different geographic origins that differ so starkly in reproductive timing (Helm 2009) that across the distribution range, some local populations will be in breeding condition at any time of the year. Another example is the blackcaps shown in Fig. 6.3. Blackcaps on the Cape Verde islands go through two full annual cycles of gonadal growth and regression and breed during two distinct breeding seasons, unlike Eurasian Blackcaps that have a single gonadal cycle and breeding season per year. Figure 6.3 shows that under identical captivity conditions, these differences were retained: Each population showed its characteristic reproductive cycle. Moreover, the differences were heritable, as indicated by the intermediate patterns in hybrids (Berthold and Querner 1993; Goymann and Helm 2014).

With greater taxonomic distance, such timing differences generally become even more evident, and links to underlying biological clocks are starting to be revealed (Taylor and Friesen 2017). For example, differences in breeding time have been associated with latitudinal clines in clock gene variants, with the most convincing examples relating to fish and insects (Hut et al. 2013; Taylor and Friesen 2017).

6.4 Isolation by the Clock

If differences in timing are underwritten by differences in the birds' biological rhythms, as in the stonechats and Blackcaps, they can become powerful isolation mechanisms and ultimately lead to speciation. For example, stonechats from differently timed populations mentioned above were crossbred with each other under identical captive conditions (Helm 2009). Like the Blackcaps shown in Fig. 6.3, the captive stonechats displayed the typical timing of their populations. Only when the breeding phases of the two populations overlapped were pairs from different populations successful in producing viable offspring (Helm 2009). Thus in the wild, such allochronic populations might already be limited in possible gene flow if they were to meet, for example through dispersing individuals.

In contrast to the well-established concept of "isolation by space," such "isolation by time" (Hendry and Day 2005) has only more recently been established as a formal idea. In wild birds, some convincing examples for a role of allochrony for speciation come from seabirds that nest colonially on islands (Taylor and Friesen 2017), for example Band-rumped Storm Petrel *Oceanodroma castro* (Friesen et al. 2007). On some islands, different parts of the Band-rumped Storm Petrel population breed sympatrically, but at completely different times of the year, and thereafter leave the colonies for the rest of the year (Friesen et al. 2007). As a consequence, these allochronically breeding petrels never meet, and the island population shows substantial genetic substructure by reproductive timing. In this example, breeders on one and the same island are in effect allopatric during reproductive seasons and have greatly diverged from each other.

Initial isolation of allochronically breeding populations has also been shown for wild birds that reproduce in neighboring locations. The Andean Rufous-collared Sparrows described above have diverged genetically, but furthermore, they show also signs of divergence in sexual signals. When song from the allochronic populations of the opposite Andean slope was played back to the local population, the receiving birds responded more hesitantly than when they heard songs from synchronic populations (Danner et al. 2011). This might suggest that avian song, which is only performed during the breeding season, may diverge quickly between populations that never hear each other sing, and thereby further accelerate allochronic isolation (Wilkins et al. 2013). Allochronic divergence of birds over short distances might be relatively common in tropical regions, where seasonality is often very local. A recent study involving 57 New World bird species related speciation to allochrony in response to different seasonal timing of food availability and ultimately precipitation (Quintero et al. 2014). Findings of comparative analyses were seen to support a so-called asynchrony of seasons hypothesis (Martin et al. 2009), which proposes that allochrony is an important contributor to the high speciation rates in the tropics.

6.5 Conclusions

Most studies on divergence between populations and on speciation have focused on spatial segregation, but recent evidence emphasizes also a role for temporal segregation. The evolutionary mechanisms are probably somewhat different because unlike spatial behavior, temporal behavior is based on innate, internal biological mechanisms. Because biological rhythms differ somewhat between individuals, they offer rich substrate for evolutionary change and can contribute to isolation and speciation, for example by mating time. The potential importance of allochrony for avian speciation might be increased by seasonally displayed mating behaviors, in particular by song, which may function as an additional isolation factor (Wilkins et al. 2013). Examples for allochronic divergence of bird populations that breed in relative proximity, so far, stem mainly from migratory species and from tropical areas. However, allochronic isolation might be more widespread and could occur, so to speak, at our door step. For example, birds breeding in urban habitats often sing much earlier in the day and reproduce far earlier in the year than conspecifics in nearby rural areas. Such behavioral differences on both time scales have been linked to the birds' biological rhythms (Dominoni et al. 2013a, b) and could contribute to decreasing gene exchange between urban and rural populations (Gill and Brumm 2013).

Further Reading

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